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Chapter · October 2000

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MATING PATTERNS, SEXUAL SELECTION AND PARENTAL CARE: AN INTEGRATIVE APPROACH

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ABSTRACT. Mating patterns, sexual selection and parental care are central topics in behavioural ecology, but they are often analysed in isolation from each other. We propose a new conceptual framework to investigate these topics in relation to each other. We argue that it is beneficial to study both mating behaviour and parental care of all types of individual in a population, because the behaviours of different individuals are interrelated in many ways. In particular, we propose a framework in which the parental care adopted is the best response to the mating behaviour and the mating behaviour adopted is the best response to the parental behaviour. The backbone of the proposed framework is the feedback relationship between mating strategies (e.g. accepting or rejecting a mate), mating opportunities (related to the number and quality of animals searching for a mate) and parental care strategies (e.g. caring for the offspring or deserting them). For instance, mating opportunities should influence both the mating and parental strategies. The mating and parental strategies, in turn, have an effect on mating opportunities. We emphasise the conceptual significance of these feedback loops as well as referring to empirical studies which have demonstrated some of these feedbacks. The strength of these feedbacks probably vary between species and may be negligible in some systems. Unlike most previous approaches to mating behaviour and parental care, we do not assume that mating systems, parental investments by males and females, operational sex ratio, reproductive rates, or the intensity of sexual selection are fixed in a population. Rather, these characteristics emerge when one specifies the behavioural options of males and females, and their consequences. Mating and parental decisions can have consequences beyond the immediate breeding attempt and the proposed framework allows us to investigate such decisions from a life-history perspective. Mating and caring decisions involve various interactions among members of a population (e.g. conflicts between prospective mates, and between male and female parents), thus studying mating and caring behaviour benefits from the use of game theory. Since the state of animals (e.g. whether they are mated or not, their age, energy reserves or the number of their offspring) and the time in the breeding season commonly influence the payoffs from different behavioural options, we advocate the use of state-dependent dynamic game theory as a suitable approach for the analysis of such decisions. Finally, we call for a new generation of theoretical models and empirical studies to understand the diverse mating and parental behaviour of animals which have fascinated evolutionary biologists from Darwin onwards.

Recommended citation: Székely T, Webb J N & Cuthill I C. 2000. Mating patterns, sexual selection and parental care: an integrative approach. *IN 'Vertebrate Mating Systems', M. Apollonio, M Festa-Bianchet & D. Mainardi (eds), 2000, World Science Press, London pp 194-223.*

1. Introduction

Sexual selection, mating patterns and parental care are topics which have generated tremendous interest in recent years. On the one hand researchers strive to understand the costs and benefits of mate choice and the various ways in which animals compete for access to mates¹⁻⁷. On the other hand they investigate the ecological, genetic and phylogenetic conditions which influence patterns of parental care^{8,9}. Vertebrates are popular subjects for these studies, since they have a great diversity both in their mating behaviour and their parental care.

However, mating patterns and parental care are often analysed in isolation from each other. For example, models often assume that parental investments of males and females (as defined by R. Trivers¹⁰), the mating opportunities (e.g. the operational sex ratio as defined by S. T. Emlen and L. W. Oring¹¹) or the mating patterns are fixed in a population of animals. In this paper we argue that it is timely to consider explicitly the feedback relations between mating and parental behaviour. In particular, to understand mating behaviour of animals we need to understand their patterns of parental care and to understand parental care we need to understand mating behaviour. In this view, mating behaviour and parental care are seen as interrelated: there is a feedback loop, with each behaviour influencing the other. It would be hard to find a better illustration of the feedback relationships than the painting 'Drawing Hands' by Maurits Escher (Figure 1): each hand is drawn by the other. Escher spent several years in Italy, thus his painting has a particular appeal when illustrating a concept presented at a conference in Sicily.

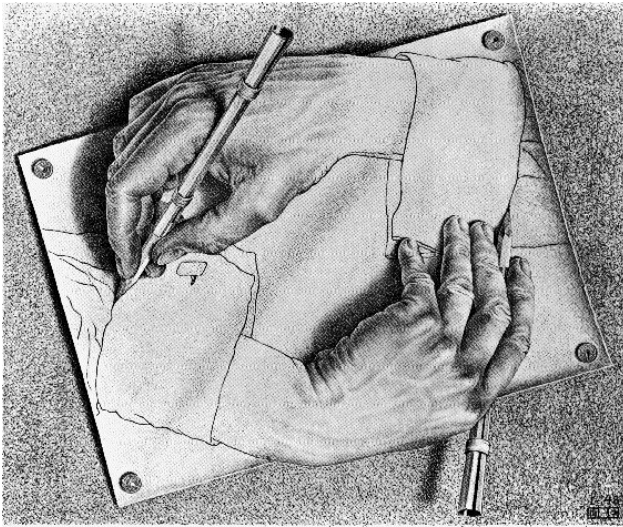


Figure 1. Drawing Hands by M.C. Escher.

Let us illustrate the significance of these feedbacks with a hypothetical example. We investigate a population of animals during the breeding season and look at a female which is courted by a male. Should she accept him or not? Her decision should depend on her gain from mating with the male and on her gain from rejecting the male and searching for other, potentially more suitable mates. Clearly, both of these gains depend on the behaviour of males. First, the behaviour of her potential mate is important, since if this male does not help her to raise her young, she may work very hard to raise only a few young. Second, the behaviour of other males in the population is also important, because her gain from rejecting this suitor depends on the number and the quality of unmated males in the population. The number of unmated males, in turn, depends on whether these males were

rejected by other females or not, and whether those males which mated decided to help their female to raise the offspring or not. Now we look at the behaviour of males and ask whether a male should spend time and energy on courting a particular female or not. His decision should depend on his gains from being accepted or rejected by the female. These gains, in turn depend upon the behaviour of his prospective mate and other females in the population.

The message here is that to understand female behaviour (whether she should accept a male or not, or care for a brood or not) we need to know the behaviour of males in the population. In turn, to understand male behaviour (whether he should court a female or not, or care for a brood or not) we need to know the behaviour of females in the population. We may assume some phylogenetically determined roles of the sexes, for instance, the females may be predisposed to care for the offspring (e.g. mammary glands in female mammals), but this assumption may be realistic in some species and unrealistic in others. Since both mating behaviour and parental care are highly variable traits both within a population and between populations, any adequate theory should attempt to explain these variations.

In this chapter we review some of the most influential models of mating behaviour and parental care. Next we outline a new theoretical framework within which these behaviours can be analysed. Although several researchers have previously thought about the feedback relations between mating and parental behaviour^{9,12,-14}, we consider a more general theoretical framework that allows us to predict the mating pattern and parental care given the interactions between mating and parental behaviour. Finally we review various aspects of the proposed framework and suggest that it may be preferable over some of the existing ones, since it allows us to relate short-term behaviours to life-history consequences and it allows us to investigate the interactions between the animals in a population.

This framework originates from the studies developed by our research team. In particular, in a series of studies we have analysed parental behaviour theoretically¹⁵⁻¹⁷, experimentally¹⁸⁻²³ and phylogenetically^{24,25}. Nevertheless, we go beyond these specific studies by proposing a conceptual framework. Our objectives here are to give a verbal account of the proposed framework and encourage research workers to investigate specific aspects of this framework theoretically and empirically. Admittedly, this paper will be biased towards birds because those are what we are most familiar with. Nonetheless, the framework we present is applicable to other organisms as well.

2. Terminology

We make a distinction between 'mating pattern' and 'mating system'. We define a 'mating pattern' as the distribution of matings in a population of adult animals during a breeding season. Thus males and females may be unmated, monogamous or polygamous (i.e. having two or more mates). This definition of 'mating pattern' follows the suggestion of I. Ahnesjö and her co-workers²⁶. The term 'mating system' (which is the equivalent of breeding system as defined by J. D. Reynolds¹²) is used to indicate a wider framework which has been considered by many workers and which may include, for example, aspects of resource distribution (e.g. 'resource defence polygyny') and the manner of mate acquisition and parental care¹¹. We define a parental care pattern as the distribution of care (i.e. biparental care, male-only care, female-only care and no care) in a population of socially mated animals. Parental care patterns may vary with the development of the offspring (for example, both parents may incubate the eggs but only one feeds the young) or with the time in the breeding season (e.g. care patterns may be different between early and late breeders).

3. Past models of mating systems and parental care

N. B. Davies wrote in his book²⁷ on the behaviour of Dunnocks *Prunella modularis* that two papers (both published in 1977) had the greatest influence on his way of thinking about mating systems and parental care. One of these papers was by S. T. Emlen and L. W. Oring¹¹ which presented a framework for understanding mating systems and the intensity of sexual selection when one knows the spatial and temporal distribution of ecological resources (such as food) as well as the parental investments (as defined by R. Trivers¹⁰) by males and females. The other was J. Maynard Smith's paper²⁸ in which he introduced game-theoretic models for understanding parental care patterns.

According to S. T. Emlen and L. W. Oring parental investments should influence the operational sex ratio (OSR), that is, the ratio of the numbers of sexually active females and males. In turn, the OSR and the distribution of resources determine the mating system and the intensity of sexual selection. For example, if all females in a population care for their young, then the OSR will be male-biased and we expect intense competition among males for access to females. Thus S. T. Emlen and L. W. Oring emphasised that the spatio-temporal distribution of resources and mates have profound effects on mating systems. Following S. T. Emlen and L. W. Oring the OSR has often been considered as a major predictor of mating competition²⁹.

Several theoretical models have been developed to refine particular aspects of this viewpoint³⁰⁻³². In some of these models the qualities of individuals may be different^{33,34}. These models assume that parental care allocations ('investment') by males and females cannot respond to mating patterns, rather they are inputs which influence mating patterns and the intensity of sexual selection.

The essence of J. Maynard Smith's²⁸ 'Models 2 & 3' argument was that the payoffs from providing care and from desertion determine whether the parents care for the offspring or desert them³⁵. Since the interests of males and females are often different ('conflict of interest'), he used game theory to find the solution. One of the major reasons for desertion (or reducing care for a particular brood) is to secure a new mate. Thus, according to this approach, mating opportunity is an input variable whereas the parental care patterns are the outputs. Since the OSR and mating patterns influence mating opportunities, J. Maynard Smith's approach assumes an opposite causality to that of S. T. Emlen and L. W. Oring.

Parental care has been analysed by two lines of theoretical studies^{8,36}. First, researchers have focussed on the behaviour of either a single individual or a single sex (i.e. male or female) and investigated the influence of various ecological and behavioural variables on the provision of care^{37,38}. For example, the effect of paternity on parental care was explored by several recent models³⁹⁻⁴¹. H. Kokko modelled the allocation of a male's resources to advertising, care provision and survival⁴². Some of these models are state-dependent, i.e. the behaviour of an animal depends on some characteristics of its situation such as its energetic reserves or the age of its brood^{43,44}. The second line is the development of game-theoretic models to investigate how the behaviour of the mate and other individuals in the population influence parental behaviour. For example, the game between a pair of animals has been analysed by various models⁴⁵⁻⁴⁸. The latter two models^{47,48}, as well as J. Maynard Smith's²⁸ Model 3 also include the effects of other population members on the behaviour of focal parents. The relations between paternity, female behaviour and parental care have also been analysed using game-theoretic models^{49,50}.

4. The proposed framework for linking mating behaviour and parental care

We suggest investigating mating behaviour and parental care within a joint framework (Figure 2). In particular, we argue that the payoffs from mating opportunities should influence the behaviour of unmated and mated animals. Mating and parental decisions, in turn, feed back to mating opportunities (i.e. the number and quality of unmated males and females in the population). In other

words, we propose a framework in which parental care is stable given the mating behaviour it generates and the mating behaviour is stable given the parental care it generates. This is a game-theoretic framework in which the optimal behaviour of a male depends on the behaviour of other males and females in the population, and the optimal behaviour of a female depends on the behaviour of other females and males in the population. In this framework the environment (e.g. distribution of resources, intensity of predation) may influence both mating and parental behaviours. Unlike previous approaches, we do not assume *a priori* any particular mating pattern, parental care pattern or intensity of sexual selection; rather these characteristics are generated by the behaviour of the animals in a given environment. We refer below to theoretical and empirical studies which show that it is important to consider these feedbacks.

This conceptual framework should not be thought of as a complete account of all mating and parental behaviour observed in the wild. Rather, we aim at directing the attention of researchers to the links between mating and parental behaviour and argue that we need a better understanding of these links. We start describing the basic framework and then move on to reason why this framework may be more suitable than some of the previous scenarios. Finally we suggest selected topics which may be investigated from the perspective of our framework.

Our framework focuses on adult males and females over a reproductive period (such as a breeding season). To do this we distinguish unmated and mated animals.

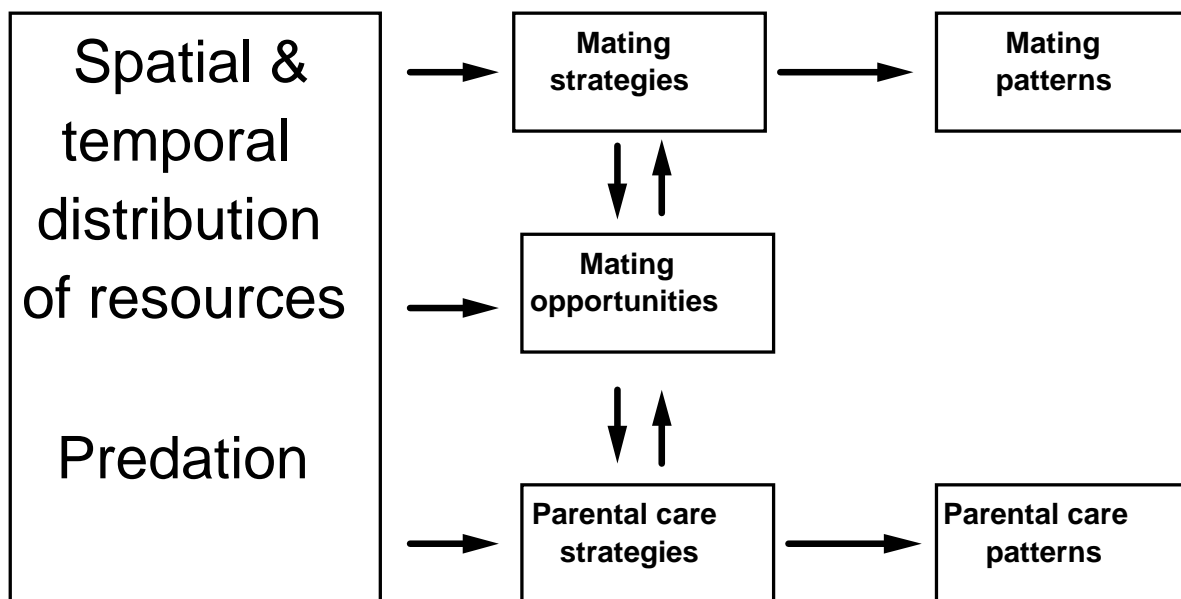


Figure 2. The proposed framework. Mating strategies refer to the behavioural decisions of unmated animals, such as to accept or reject a mate. Parental care strategies are the behavioural decisions of mated animals, such as to care for a brood or desert them. Males and females may have different mating and parental care strategies. The mating and parental care strategies generate the mating patterns (i.e. the distribution of matings in the population, e.g. monogamy, polygyny, polyandry) and the parental care patterns (i.e. the distribution of parental care in the population, e.g. biparental care, female-only care, male-only care).

4.1. Feedback relations between mating and parental strategies

Mating strategies. Unmated animals search for a mate and if they find one then they either accept or reject it. Mating occurs if both the male and the female accept each other, i.e. the choice is mutual. If they mate, then the male and the female go on to produce young.

The mating strategies of males and females should be influenced by the payoffs from reproducing with a potential mate and from searching for another mate. The latter payoff depends on the mating opportunities: the quality of potential mates and the cost of mate search (which may be in time, energy or survival). For example, if the prospects for finding a new mate are low, either because there are few potential mates in the population or the cost of searching for a mate is high, then the animal may be better off accepting a mate even if it is of low quality⁵¹.

However, mating opportunities and the quality of potential mates cannot be assumed at the outset, but are determined by the mate choice strategy adopted by population members. Therefore, mate choice is a game-theoretic concept. First, if there is choice by both sexes then the best mate choice strategy of an individual depends on which members of the opposite sex are prepared to accept that individual. Thus the best strategy for a male of a given quality depends on the strategy of all females; and the best strategy of a female of a given quality depends on the strategy of all males^{34,52,53}. Second, on mating, pairs are removed from the pool of potential mates. Thus the number and quality of each sex at a given time depends on all previous mate choice decisions of all members of the population^{53,54}. (For further discussion of mate choice from a game-theoretic viewpoint see⁵⁵).

Parental care strategies. Once the animals have produced young they decide whether they will care for the offspring or desert them. The optimal decision is determined by the payoffs from caring and from deserting. The payoff from caring may be an increased survival of the young and the chance of retaining the mate for future breeding^{8,36}. For example, the payoff from raising the young depends on the number and the quality of offspring, the ability of the young to reach reproductive age (given the male, the female, neither or both parents care for them) and on the genetic relatedness between the offspring and the parent. Mate retention is advantageous if mate search is costly, if experienced pairs (i.e. the ones who have already bred together) achieve higher reproductive success than inexperienced ones or if the mate is of high quality⁵⁶⁻⁵⁸. Mate retention may also be important when nest predation is high, since the pair can quickly lay a replacement clutch⁵⁹. The payoff from deserting is based upon the chance to reproduce with a new mate or to improve survival until future breedings^{36,60}.

Observations and experiments suggest that mating opportunities often influence whether an animal cares or deserts. For example, mating opportunities may decrease near the end of the breeding season when the chance of a successful new brood diminishes^{23,61}. In addition, late breeding females often help their mate to incubate in polyandrous shorebirds (Spotted Sandpipers *Tringa macularia* and Dotterels *Eudromias morinellus*), whereas normally a female does not provide care after she has laid her eggs^{61,62}.

Mating opportunities have been experimentally manipulated in fish and birds. Male Starlings *Sturnus vulgaris* decreased their parental care in response to increased mating opportunities⁶³. Male cichlid fish deserted their nest at a female-biased sex ratio and spawned with a new female^{48,64}. Similarly, in St. Peter's fish *Sarotherodon galilaeus*, a mouth-brooding cichlid, females deserted their nest more often at a male-biased sex ratio than at an equal or female-biased sex ratio⁴⁸, although in another cichlid fish M. H. A. Keenleyside was unable to induce female desertion by creating a male-biased sex ratio⁶⁴.

However, in many animals parental care is not as flexible as it is in fish. For example, in most mammals the female has to gestate and suckle the offspring for a long period of time, whereas

the male appears to be more free to desert. Nonetheless, the feedbacks may also be important in these animals too. For example, if the male gains less by searching for new mates than by helping his mate e.g. by providing food for her or defending his mate and young from intruders, then we expect that the male will stay with his mate and help her to raise the young^{65,66}. Such decisions have implications both for the pattern of parental care (female-only care vs. biparental care) and for the mating pattern (polygyny vs. monogamy).

State-dependent behaviour. Both mating behaviour and parental care may depend on the states of individuals, i.e. on short-term and long-term differences between the animals. Short-term differences such as body reserves often influence mating and parental behaviour. For example, in a model of mating and parental care in birds J. N. Webb and his co-workers predicted that parents with medium body reserves should care for their offspring, whereas ones with either low or high body reserves should desert¹⁷. Parents with high body reserves desert to find a new mate and initiate a brood whereas parents with low reserves desert because the continuation of care would risk their own survival⁴⁴.

Consistent individual differences ('qualities'; e.g. attractiveness, ability to provide care) may also influence mating and parental care. For example, experimentally created 'attractive' males fed their chicks less in the Zebra Finch *Taeniopygia guttata*⁶⁷ Barn Swallow *Hirundo rustica*⁶⁸ and Collared Flycatcher *Ficedula albicollis*⁶⁹ although it is not clear whether the attractive males reduced their share, or their mate increased her share of feeding. These experimental results have usually been interpreted as the latter, with greater care by the mate in response to presumed higher (genetic) quality of offspring (i.e. "differential allocation hypothesis"⁶⁷). The alternative interpretation of such results (compensatory feeding by a mate whose partner now gains more from pursuing additional mating opportunities than by helping raise the current brood) is equally plausible.

The appropriate approach for analysing the influence of states on the behaviour of animals is stochastic dynamic programming (SDP^{55,70-72}). In such models the various behaviours (e.g. mating, caring) which contribute to reproductive success may be analysed using a common currency. SDP has been successfully used to model a variety of mating and caring behaviours^{17,43,44,73}.

Feedbacks between mating and parental care. The essential feature of the proposed framework is the feedback loop between mating strategies, mating opportunities and parental care strategies (Figure 2). The payoffs for a given mating strategy clearly depend on mating opportunities and the care strategy. First, the number and quality of unmated males in a population and whether the potential mates cares for the brood or not determine the payoffs for accepting or rejecting the mate. Second, the payoffs for deserting also depend on the mating opportunity, that is, the payoffs for a deserting male are higher in a female-biased environment than in a male-biased one (see Parental care strategies).

However, both caring decisions and mate choice have consequences for mating opportunities. First, when a male deserts his brood and searches for a new mate this changes the mating opportunities of all animals in the population. In particular, the mating opportunity increases for the females, whereas it decreases for males. Also, after the young become independent the parents may either remain together or divorce. These choices again should influence the number and quality of unmated animals, i.e. the mating opportunities. Second, when an animal accepts a mate then the number of unmated animals is reduced. Accepting or rejecting a potential mate also influences the quality distributions of unmated animals in a population. For example, if the best

males pair up early in the season, then a late-arriving female may have to accept a low quality mate⁵⁴.

The mating opportunities also influence the competition for mates and thus the interactions within and between sexes. For example, it has been shown that at a male-biased sex ratio aggressive interactions were more common among male Sand Gobies *Pomatoschistus minutus* than at a female-biased sex ratio⁷⁴. In addition, at a male-biased sex ratio only the largest males were able to build nest and attract females, whereas at a female-biased sex ratio there was no difference in size of the nest-building and non-building males.

The feedbacks between mating opportunities and caring strategies may have a profound effect on parental behaviour. We have illustrated this point with a game-theoretic model¹⁶. This model is based upon J. Maynard Smith's²⁸ Model 2, but explicitly investigates two breeding attempts by both the male and the female. In the model of J. N. Webb and his co-workers¹⁶ the animals can mate and breed twice but can only provide care for one brood. Both the male and the female may either care for the brood or desert. Should they care for their first brood or desert? This depends on their probabilities of having a second brood and on the behaviour of both their current mate and their new mate. For example, the male should desert his first brood if his payoff from deserting, finding a new mate and raising a second brood is higher than his payoff from caring for the first brood. The condition for desertion can be expressed in the following way: the probability of finding a new mate should be greater than some positive value determined from the payoffs for biparental, uniparental and no care. Let us suppose that the optimal behaviour of the female is caring for her first brood. It is easy to find parameter values which satisfy the condition of female-only care (and desertion by males). However, this condition cannot be satisfied if one considers the feedback between parental strategy and mating opportunity. In particular, if all females care in the population (and we assume that no female enters the population to breed), then a deserting male has no chance of finding a new mate and reproducing. Therefore, the condition for desertion cannot be satisfied. Similar logic applies for male-only care.

Dynamic games. It is often essential to investigate the various feedback loops between the behaviour of males and females^{47,75} as well as between mating and parental behaviours. The analyses of such situations require dynamic games i.e. using dynamic optimisation when the fitness of the animals depend on the behaviour of other animals in the population^{76,77}. For example, recently S. H. Alonzo and R. R. Warner analysed the mating and the caring behaviour of the Mediterranean Wrasse *Symphodus ocellatus* using a dynamic game model⁷⁸. In this fish some males build a nest and attract females to their nest, whereas other males ('sneakers') do not build a nest but try to fertilise the eggs laid into other males' nests⁷⁹. The number of sneakers at a nest influences the behaviour of the nesting males as well as the behaviour of females⁸⁰, since the nesting male and the females prefer to spawn in the absence of sneakers. Female behaviour also depends upon the expected care by the nesting males, since if the nesting male decides to desert his nest then the unguarded eggs have no chance of surviving. The female behaviour in turn influences the behaviour of sneakers, since the sneakers prefer those nests with high past mating success. Finally, the caring behaviour of nesting males depends on how many females spawned in their nests, thus the males' behaviour is contingent on the mate choice of females as well as on the distribution of sneakers among nests.

It is not straightforward to find the optimal mating and parental behaviour in the Mediterranean Wrasse, since we cannot use the standard approach and assume that the behaviours of nesting males, sneakers or females are fixed. In fact, Alonzo & Warner (MS)'s model shows that optimizing the behaviour of all fish vs. fixing the behaviour of one set of players (i.e. sneakers, females or nest males) lead to very different predictions.

As we argued above, the states of the animals and the interactions among the individuals all influence the payoffs for mating and caring strategies and we advocate the use of dynamic games for analysing such decisions. A major feature of these models is that the costs and benefits of mate choice and care are not given at the outset, but are generated by the actions of the animals over a period of time such as the breeding season^{15,55,77,78}.

4.2. *Inputs and outputs*

Resources and predation. The spatial and temporal distribution of resources and predation often influence mating and parental care strategies. If the distribution of resources is patchy then this may induce a clumped female distribution as has been argued for many mammals⁸¹⁻⁸³. The clumped female distribution, in turn, makes the defence of several females by a single male economic. Also, the abundance of resources such as food is expected to influence whether a single parent is able to care for the young or not. For example, it has been found that on the territories of polygynous Great Reed Warblers *Acrocephalus arundinaceus* prey abundance was higher than on territories of four monogamous warbler species⁸⁴. In all five warblers they found that the male fed the chicks, although male Great Reed Warblers fed the young less often than males of the monogamous warblers. These results suggest that a single parent is better able to cope with provisioning the nest when prey abundance is high.

These aspects can be incorporated into our framework. For example, the effect of the resources on mating and parental behaviour may be analysed by state-dependent stochastic modelling^{17,44,73}. The effect of the resources may be more complex than often acknowledged and formal models may produce intuitively unexpected results. For example, prey abundance may not only influence the ability of a single parent to cope with care⁸⁴, but may also influence the cost of parental care. Thus the survival of the parent from after the young fledge until future breeding seasons may be higher when prey abundance is high, because the parent does not work as hard as when prey abundance is low. The mortality of the caring sex in turn influences the adult sex ratio in future breeding seasons, thus it has a bearing on mating opportunities. Also, prey abundance may influence the number of birds entering a site to breed. For example, sites where prey are abundant may attract more adults to settle than poor sites, thus mating opportunities may be initially better in a good site than in a poor one.

Predation also influences mating and caring strategies as well as the adult sex ratio. For example, female Sand Gobies have clear preferences for large and colourful males in the absence of predators, whereas they do not show a preference in the presence of predators⁸⁵. Since the risk of predation is often a major cost of mate search, courtship and mating, the presence of predators often reduces the intensity of courtship and nest-building behaviour⁸⁶⁻⁸⁸. Finally, if mating or caring is more costly for one sex than the other then this may change the adult sex ratio. For example, increased mortality of parents because of predation is common, since pregnant females and parents provisioning and defending young are often taken by predators^{8,89}.

Mating patterns and sexual selection. Mating patterns are generated by the behaviour of unmated males and females. Based on the mating patterns one may calculate an index of the mating skew⁹⁰. Such an index, in turn, may indicate the intensity of sexual selection. For example, if each male mates with a single female during a reproductive period, then the intensity of sexual selection is weak. In contrast, if a few males monopolise most matings in a population then the competition between males for access to females is intense.

Parental care patterns. Patterns of parental care and reproductive rates emerge as the result of the behaviour of mated animals. These patterns may vary with the age of the offspring and may depend on the state of the animals. The reproductive rates may be evaluated for both males and females by estimating the time required to find a suitable mate and reproduce with the mate. These rates, as produced by the mating and caring behaviour of adults over the breeding season, may be different for males and females if the adult sex ratio deviates from unity or if the duration of the breeding is different for males and females^{30,47}.

5. The significance of life-histories and game theory

The proposed framework extends previous approaches to mating behaviour^{11,82} in three ways. First, it allows us to investigate the behaviour of both unmated and mated animals in an explicit life-history framework. In particular, it is possible to construct models which investigate how the behavioural decisions affect various life-history trade-offs. For example, unmated animals may trade off mating against surviving until future years. Parental care may also involve several trade-offs such as caring for the young or deserting and improving the survival of the parent. Since these trade-offs often depend on the state of the animals, state-dependent life-history theory may be the appropriate approach to analyse such decisions⁹¹. Second, the proposed framework allows us to investigate the interactions between animals, e.g. within and between sexes. These interactions are important, since the interest of individuals are often different. For example, male and female parents may have a conflict over who should provide the care for the offspring. In addition, some payoffs may depend on the behaviour of other population members (i.e. mating opportunities). Analysing such situations requires a game-theoretic approach. Although single-sex approaches to mating systems such as matrix based demography⁹² are very valuable, we believe that complete understanding of mating and parental behaviour require game-theoretic analyses. Third, we have various feedbacks in this framework, whereas most current models do not emphasise these feedbacks. For example, the standard model of mating systems considers only influences in one direction (i.e. the distribution of resources determines the distribution of females and the distribution of males) and there is no effect in the opposite direction. Clearly, mating behaviour of females is often influenced by how much care they expect from their mate²⁷, thus the mating strategies of females should depend on the behaviour of males. The strength of these feedbacks may vary between organisms and may be constrained by phylogeny (e.g. in many fish, amphibians and birds either sex is capable of caring for the offspring unassisted, whereas in mammals the offspring initially depend on their mother), although we emphasise that we can not exclude any of these relations *a priori*.

6. Beyond the basic framework

The basic framework is not intended to include all the subtle details of mating and parental behaviour which stimulated much research in recent years, although we are convinced that it is a useful starting point for investigating various topics. We envision that the basic framework may be extended in various ways and here we outline some of these. We are fully aware that each of these extension may be challenging on its own right and require collaboration between theoreticians and empiricists.

6.1. Behavioural options

Mating behaviour and parental care are more diverse than we have discussed so far. For example, unmated animals may use different tactics to obtain mates (e.g. court, harass, sneak). Also, males are

often confronted with the decision of whether to guard a mate or to pursue additional mates⁹³. These choices need not be mutually exclusive; in other words a male may spend some time guarding his mate and the rest of the time pursuing additional mates.

Parental care is more than just deciding about caring or desertion. For example, parents often provide care on a continuous scale. Also, they may provide different types of care for their offspring such as guarding, brooding, defending or feeding. In addition, males and females may carry out different types of care: e.g. in many passerines only the female incubates whereas both the male and the female feed the young.

These aspects of mating and care strategies can be readily investigated from the perspective of the proposed framework by specifying appropriate behavioural options and consequences. Nevertheless, mating and care strategies may interact in a complex way. For instance, a monogamous male may have the option of either providing care for his current mate or searching for a new mate. If he finds a second mate, he has the option of either guarding his new mate or helping his first mate to raise the offspring. Finally, if both of his mates have produced some young then he faces a choice of how to split parental effort between the two broods⁹⁴. All of these decisions should depend on the expected behaviour of his potential mates, which in turn, should be related to these females' chances of getting another, perhaps better, male. Finding the optimal mating and caring strategies may be even more complicated if the females interact with each other, e.g. if the female of the mated male attempts to prevent her male from pairing with a new mate^{95,96}.

6.2. Trade-offs between mating and caring

Although caring for young and attracting a new mate are often traded off against each other in birds⁶³, this trade-off may not exist in other animals such as fish. For example, in some species males are able to attract new mates while guarding eggs in their nests^{97,98}. In fact, the presence of eggs appears to make the male more attractive. This situation may be analysed by re-defining the behavioural options of the male and allowing it to simultaneously care for a clutch and attract a new mate⁴³.

6.3. Genetic relatedness between parents and offspring

Recent studies have demonstrated that genetic and social mating patterns may be different. On the one hand, extra-pair fertilisations are common in many animals, and the male parent often raises young which are sired by other males^{6,93,99,100}. On the other hand, intraspecific nest parasitism, brood parasitism and brood amalgamation also occur in many animals. So it is possible that neither the male nor the female raise their own offspring¹⁰¹. Some of these aspects may be incorporated into the proposed framework by allowing the payoff from parental care to depend on the relatedness between offspring and parent.

6.4. Signalling parental ability

Parents may signal their abilities to provide care and this may influence their success in attracting a mate. For example, female Fifteen-spined Sticklebacks *Spinachia spinachia* prefer males which fan their nests often¹⁰². This seems a reasonable decision rule, since the male pumps fresh water into the nest by fanning and thus fanning is correlated with hatching success¹⁰². From a single animal's point of view the optimal level of signalling (which may use resources which could be used for caring or surviving, cf. H. Kokko⁴²) should depend on the signalling level of other animals in the population.

6.5. Temperature-dependent reproductive rates

In many ectotherms, such as fish and amphibians, the reproductive rates depend on the ambient temperature^{5,29}. For example, in the pipefish *Syngnathus typhle* and Midwife Toad *Alytes muletensis* the reproductive rate of males increases with temperature whereas the reproductive rate of females does not^{103,104}. The influence of these relations on mating patterns and parental care may be investigated by allowing the developmental time of young to depend on temperature. Given these developmental times and mating times (e.g. searching for mate, laying the eggs) the reproductive rates can be calculated for males and females in a similar fashion to mating patterns and parental care patterns.

6.6. Process of decisions

Most models of mate choice and parental care assume that the males and females have one or few interactions. In reality the animals repeatedly interact and they probably assess each others' intentions through such interactions. For example, it has been observed that in St. Peter's fish the parents circle above the fertilised eggs for up to 45 minutes⁴⁸. This delay is dangerous, since unguarded eggs are quickly predated. Once one of the parents starts picking up the eggs, the other normally quickly follows it. One interpretation of this delay is that the parents 'argue' about who should make the first move in picking the eggs. The theoretical counterpart of this empirically observed bargaining process is that the evolutionarily stable pattern of care arrived at through the bargaining process may be different from the one which would be predicted for a single interaction¹⁰⁵.

7. Conclusions

R. Trivers, S. T. Emlen and L. W. Oring, and J. Maynard Smith have provided powerful research paradigms which successfully stimulated much research about the mating and parental behaviour of animals. Now it is timely to take a fresh look and approach mating and parental behaviour in an integrated way. In particular, we propose a framework in which mating patterns, mating opportunities and parental care patterns are explicitly interrelated. Since both mating and parental behaviour often depend on the state of the animals and on the interactions within and between sexes, we advocate the use of dynamic game theory. To understand the relations between mating and parental behaviour we encourage researchers to develop theoretical models and carry out observations, experiments and comparative studies.

8. Acknowledgements

TS was supported by NERC grant 'GR3/10957' to AIH, ICC and JMM and an OTKA grant (T020036). TS would like to thank Marco Apollonio and Marco Festa-Bianchet for their invitation to the Workshop. The ideas in this paper were developed in conjunction with Alasdair I Houston and John M McNamara. We thank Alasdair I Houston, John M McNamara, Suzanne H Alonzo, Marco Apollonio, Sigal Balshine-Earn, Marco Festa-Bianchet, András Liker, John D Reynolds and David F Westneat for their comments on the manuscript.

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